

Scanning Electron Microscopical Studies on the Spores of Pteridophytes

XI. The Family Oleandraceae (*Oleandra*, *Nephrolepis* and *Arthropteris*)

by

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Abstract

The monolete bilateral spores of three genera of ferns belonging to the Oleandraceae (*Oleandra*, *Nephrolepis* and *Arthropteris*) were examined by scanning electron microscope. It is found that the spores of *Oleandra* are characterized by a large folded perine, and densely echinate exine bearing pointed spines or blunt supporting rods. *Arthropteris* possesses spores with more or less similar perine characteristics, and considering its morphological similarities with those of *Oleandra*, this genus may well be included in the family Oleandraceae. Spores of *Nephrolepis*, on the other hand, being characterized by insulate or verrucose perines, thus resemble more closely those of the Davalliaceae, the closest relative of *Nephrolepis*. However, many of its morphological and anatomical characteristics are so distinctive and unique that it clearly constitutes a natural group by itself, and should, as proposed by Ponce de Leon (1953), be treated as the only member of an independent family, the Nephrolepidaceae.

Introduction

The taxonomic and phylogenetic position of the fern genera *Oleandra*, *Nephrolepis*, *Arthropteris* and *Psammiosorus* have long been debated and remain controversial. *Oleandra* Cav. is a genus of the tropics and has about 40 species. It differs from other fern genera in many features, and for that reason its taxonomic position is not fully established. Attributing great importance to the articulation of the stipe to the stem J. Smith (1866) first segregated *Oleandra* from the Aspidiaceae and considered it the sole genus of the new tribe of Oleandreae. After the detailed anatomical study of the Japanese species *O. wallichii* by Ogura (1938), *Oleandra* was considered as an isolated genus, and treated as the only genus in the family Oleandraceae (Ching, 1940). Later, many authors accepted it as a monogeneric family (Dickason, 1946; Ponce de Leon, 1953; Pichi-Sermolli, 1965). Others however, have either treated it as 'a genus incertae sedis' (Bower, 1928), or placed it among many other groups of ferns. Of the latter Diels (1889) arranged it in the independent monotypic Tribus Oleandreae of Polypodiaceae, and Christensen (1938) put it in the monotypic subfamily Oleandroideae of the same family. Still other pteridologists included it in the Dennstaedtiaceae (Holttum, 1947), in the Davalliaceae (Copeland, 1947; Alston, 1956; Tardieu-Blot, 1958), or in the subfamily Oleandroideae of Davalliaceae (Tindale, 1961; Crabbe, Jermy & Mickel, 1975).

The genus *Nephrolepis* Schott has about 30 species distributed in the tropics, Japan and New Zealand. Presl (1836) included *Nephrolepis* in the section Nephrodiariae of his tribe Aspidiaceae. Most workers placed it either in the family Davalliaceae (Ching, 1940; Dickason, 1946; Copeland, 1947), or included it in a separate group placed near the Davalliaceae (Nayar, 1970; Holttum, 1971, 1973). However, Ponce de Leon (1953) established the family Nephrolepidaceae for this group of ferns. *Nephrolepis* is usually classified with *Oleandra* because "they are

probably more nearly related together than either is to any other genus" (Holttum, 1954).

Arthropteris J. Smith is a small genus of about 20 species and distributed in the Old World tropics and southwards to Australia and New Zealand. "The species of *Arthropteris* are in utter confusion" (Copeland, 1958). The affinity of *Arthropteris* is not clear either (Holttum, 1966). It has certain characteristics which are similar in some extent, to the genera *Oleandra*, *Nephrolepis*, *Davallodes*, *Elaphoglossum*, *Thelypteris*, *Teratophyllum*, *Ctenitis* and *Tectaria*. It is usually placed near *Nephrolepis*, but may not be its nearest relative (Holttum, 1966).

The monotypic genus *Psammiosorus* C. Chr. of Madagascar is peculiar and shows features in common with *Arthropteris* (Copeland, 1947) and the Davallioid ferns (Christensen, 1932; Holttum, 1966). It is always grouped with the Davallioids or Oleandroids (Pichi-Sermolli, 1965), but its actual taxonomic position and affinities are not clear.

These four genera have in the past and recently been variously grouped (Holttum, 1966, 1971; Nayar, 1970; Sen & Sen, 1973; Crabbe, Jermy & Mickel, 1975): in one family, the Oleandraceae; in two separate families, the Oleandraceae (*Oleandra*) and Davalliaceae (*Nephrolepis*, *Arthropteris* and *Psammiosorus*) or in more than two families (Oleandraceae, Nephrolepidaceae and Davalliaceae). In view of the controversy regarding the taxonomic problems and phylogenetic relationships of these genera, it was thought that a detailed study of them is a project worthwhile to undertake.

Spores of ferns are becoming increasingly important in fern taxonomy (Nayar, 1964; Wood, 1973; Moe 1974; Liew, 1976c). Because they offer both reliable and stable morphological characters in (i) distinguishing species in some genera, (ii) in differentiating genera, subgenera and characterizing families (Brown, 1960; Liew, 1976b) and (iii) in the tracing of possible phylogenetic relationships and trends of evolution between taxa (Brown, 1960; Sorsa, 1964; Nayar & Dewi, 1968; Wagner, 1974) the present author decided to investigate this character and use it as a means to tackle the problems raised above. Scanning electron microscopical observation is preferred and undertaken because it offers the combined superiority of greater depth of field, high resolution, and visually presents three dimensional topographical information which reveals subtle and spectacular structures of spore surfaces previously unobtainable with the optical microscope.

Materials and Methods

Spores of the three genera of ferns belonging to the Oleandraceae (*Oleandra*, *Nephrolepis* and *Arthropteris*) were taken either from fresh plant material collected in the fields or from herbarium sheets deposited in many institutions (NY, SING, TAI, KLU and HK; see Table I for details). Fresh fronds were carefully dusted for their spores and spores from herbarium specimens were obtained with the use of clean tooth picks.

Before making scanning electron microscopical observation spores of each species are dispersed in a drop or two of Hoyer's solution (Anderson, 1954) and checked preliminary for their proper identity under an ordinary light microscope. Details of the method of preparation and observation on scanning electron microscope were as described before (Liew, 1976a). Many models of scanning scopes were employed in the present investigation, e.g., JOEL JSM 15, JSM U3, Cambridge S4-10, and Hitachi MSM 4. Black and white photomicrographs were recorded on ordinary 120 negative or on Polaroid films with (105 P/N, 55 P/N) or without (42, 107) negatives. Sizes of spores were measured either in polar x equatorial axes (P x E) or in polar x longest equatorial x shortest equatorial axes (P x E1 x E2). Values given are averages of five to ten readings.

TABLE I. Taxa of Oleandroid ferns studied in the present investigation together with some of their spore characteristics.

| Taxon | Locality ¹ , Collector, Number and Herbarium | Size (PXE) ² in μ | Sculptine Characteristics ³ |
|--|---|----------------------------------|--|
| <i>Arthropteris</i> J. Smith | | | |
| 1. <i>articulata</i> (Brack.) C. Chr. | Fi: A. C. Smith 6861 (NY) | 28-36 x 40-51 | al; b5, 7, 11; d4 ⁴ |
| 2. <i>beckleri</i> (Hook.) Mett. | A: E. F. Constable P3920 (SING) | 32-40 x 41-55 | al; b3, 11, 15; d4 |
| 3. <i>dolichopoda</i> v.A.v.R. | NG: H. W. Simmonds, s.n., Jul. 5, 1937 (SING) | 28-38 x 40-52 | al; b3, 6, 15; d4 |
| 4. <i>monocarpa</i> (Cardenay) C. Chr. | E: R. E. G. Pichi-Sermolli 6781 (KLU) | 38-46 x 41-50 | al; b4, 9, 15, 16; d4 |
| 5. <i>obliterata</i> (R. Br.) J. Sm. | Bo: J. & M. S. Clemens 27383 (NY) | 36-50 x 43-64 | al; b3, 8, 10, 11, 15; d4 |
| 6. <i>pallisotii</i> (Desv.) Alston | Fa: M. T. Kao 3731 (TAI) | 30-39 x 45-53 | al; b3, 10, 11, 15; d4 |
| 7. <i>repens</i> (Brack.) C. Chr. | Bo: J. & M. S. Clemens 29568 (SING) | 34-44 x 45-58 | al; b10, some 12, 15; d4 |
| 8. <i>tenella</i> (Forst.) J. Sm. | A: M. S. Clemens, s.n., Jan., 1945 (NY) | 45-56 x 50-65 | al; b10, 11, 13; d4 |
| 9. <i>wollastonii</i> (Ridl.) Holttum | Ph: E. B. Copeland 155 (SING) | 31-43 x 41-54 | al; b3, 10, 16; d4 |
| <i>Nephrolepis</i> Schott | | | |
| 10. <i>acutifolia</i> (Desv.) Christ | Ma: B. E. G. Molesworth-Allen 2575 (SING) | 20-24 x 27-33 | b2, 3, 17 |
| 11. <i>biserrata</i> (Sw.) Schott | Fa: F. S. Liew 10197 (TAI) | 18-24 x 23-29 | b2, 3, 17 |
| 12. <i>cordifolia</i> (L.) Presl | Ma: E. A. Turnau 839 (KLU) | 20-25 x 23-30 | b2, 3 or 4, 17, some 20 |
| 13. <i>davallioides</i> (Sw.) Kze. | Ma: B. C. Stone 7244 (KLU) | 21-27 x 25-32 | b2, 3 or slightly 3, 17 |
| 14. <i>dicksonioides</i> Christ | Ma: B. C. Stone 5895 (KLU) | 20-23 x 29-33 | b2, 3, 17 |
| 15. <i>exaltata</i> (L.) Schott | Hi: C. N. Forbes 2108M (NY) | 23-29 x 30-37 | b2, 3, 17; d4 |
| 16. <i>falcata</i> (Cav.) C. Chr. | Ma: R. E. Holtum 9820 (SING) | 18-22 x 24-28 | b2, 3, 17; d4 |
| 17. <i>hirsutula</i> (Forst.) Presl | Fa: F. S. Liew 9060 (TAI) | 18-25 x 28-35 | b2, 18; d4 |
| 18. <i>lauterbachii</i> Christ | NG: Butten, s.n., 1919 (SING) | 17-21 x 26-32 | b2, slightly 3, 19 |
| 19. <i>pectinata</i> (Willd.) Schott | CR: W. C. Burger & R. L. Lieser 6854 (NY) | 20-25 x 26-38 | b2, 3; d4 ⁵ |
| 20. <i>radicans</i> (Burm.) Kuhn | Ma: A. Samat 550 (KLU) | 17-22 x 25-31 | b2, 18; d4 |
| <i>Oleandra</i> Cavanilles | | | |
| 21. <i>madagascariica</i> Bonap. | Mr: B. C. Stone 7883 (KLU) | 25-30 x 30-40 | b8, 11; c13; d4 |
| 22. <i>neriiformis</i> Cav. | Ph: B. F. Henaez, s.n., Nov. 16, 1970 (TAI) | 30-36 x 38-45 | b5, 11, 12, 21; c12 or 14; d4 |
| 23. <i>pistillaris</i> (Sw.) C. Chr. | Ma: S. C. Chin 181 (KLU) | 31-38 x 45-55 | b11, 12; c14; d4 |
| 24. <i>undulata</i> (Willd.) Ching | Hn: F. A. McClure 20061 (NY) | 26-31 x 30-37 | b5, 12, 21; c14; d4 |
| 25. <i>wallichii</i> (Hk.) Presl | Fa: M. T. Kao 6317 (TAI) | 25-33 x 37-44 | b12 &/or 13; c14; d4 ⁶ |

1A, Australia; Bo, Borneo; CR, Costa Rica; E, Ethiopia; Fi, Fiji; Fa, Formosa; Hi, Hawaii; Hn, Hainan; Ma, Malaya; Mr, Madagascar; NG, New Guinea; Ph, Philippines.

2 PXE = Polar axis x Equatorial axis.

3 a, perine; b, same, outer layer; c, same, inner columnar layer; d, exine layer.

4 1. thick, 2. thin, 3. rough (surface), 4. smooth, 5. lophate (with large polygons); 6. with processes, 7. processes short, rounded, 8. processes small, short, 9. with many folds, 10. with amorphous or irregular structures (raised ridges &/or irregular foldings), 11. with many holes; 12. spines short, pointed, 13. spines long (up to 5 μ), pointed, 14. blunt clubs (up to 3 or 4 μ tall); 15. easily sloughed off, 16. easily cracks open; 17. with insulate, broad, interconnected ridges or verrucae, 18. ridges or verrucae insulate, small, 19. ridges or verrucae insulate, large; 20. verrucae or tubercles very prominent and protruding, 21. same, especially in lacuna, and some forming raised ridges.

5 Spores appear similar to the spores of *Oleandra* species. 6 Sculpture of spores rather variable.

Results

The sizes and general characteristics of the spores of all the species of these Oleandroid genera studied in the present investigation are given in Table I.

The insulate or verrucose spores of *Nephrolepis* clearly form a natural group by themselves (Plates I and II). These ellipsoid bilateral spores are monolete and mostly concavo-convex in lateral view. A few of them are plano-convex. The average size of the spore measures about 17–29 x 23–38 x 14–29 μ . Under the SEM, a broken outer sporoderm will reveal the inner exine layer of the spore, which is psilate, slightly scabrate or undulating (Plate I, fig. 8). The laesura is slightly raised, thin and with a short ridge in some species (e.g., in *N. pectinata* and *N. davallioides*) or thick and forming long and rough ridges in others (e.g. in *N. acutifolia* and *N. biserrata*). The sculptine or sporoderm has on its surface elements of various sizes, from small grains or humps to large tubercles, or with irregular excrescences or raised ridges of various sizes.

The ellipsoid spores of *Oleandra* are totally different from *Nephrolepis* (Plates III and IV). They are monolete bilateral spores, and are plano-convex to slightly biconvex in lateral view. The amb is oblong in shape. All the spores have a thick, prominent, loose and wrinkled perine which anastomoses to form regular or irregular polygons or lophate sculptures. Depending upon the species concerned, the perine may have spinulose, blunt or dentate excrescences. The size of the spore is 25–42 x 30–55 x 26–32 μ . Scanning electron micrographs of broken sporoderms reveal that the outer layers are built on stilts, and are supported by numerous rods connected to the layer(s) down below. These micrographs also reveal the smoothness of the inner exine in many cases (Plate IV, fig. 40). Spores of *Oleandra* may differ in sculptural details, even within the same species, but they nevertheless form a group with a unique and distinctive general pattern.

Spores of *Arthropteris* have a thick perine of various sculpturing ornamentations (Plates V and VI). Foldings may be high or low in profile, and are covered with minute projections or interlacing networks. Some *Arthropteris* spores (e.g. *A. articulata*) closely resemble those of *Oleandra* species. The outer perine of most of the spores of *Arthropteris* sloughs off easily, leaving behind the naked exine with smooth surface and laesura. The size of the spores range 28–56 x 40–65 x 25–30 μ . It is ellipsoid and sometimes roundish in polar view, and plano-convex to concavo-convex in lateral view.

Discussion

I. *Nephrolepis*

From our studies on eleven taxa of *Nephrolepis* gathered from various parts of the world it is demonstrated that the bilateral spores of *Nephrolepis* species are rather uniform and form a clear-cut group by themselves. They have thin perine and verrucose sculptine with elevations of various sizes, from slightly raised ridges to conspicuous tubercles.

In the literature, spores of many species of *Nephrolepis* have been studied. Holttum (1954) mentioned that spores of *Nephrolepis* have slightly and irregularly roughened surfaces, and are without distinctive markings. Hannig (1911) pointed out that "a perispore is unlikely to occur" in *Nephrolepis* (*N. exaltata*). This is contradicted here as shown in Plate I, fig. 8, which clearly shows the presence of an outer layer. Among the many authors who have examined the spores of *Nephrolepis exaltata* (L.) Schott was Selling (1946) who investigated Hawaiian species and described it as having very irregular warts and short, irregular ridges, with a size of 24–28 x 41–50 μ . Earlier workers have similarly investigated the spores of this species but did not mention the sculpture patterns. Marquesan (southeastern

Polynesia) spores of this taxon are $\pm 34 \mu$ in length, and with the surface conspicuously tuberculate (Brown & Brown, 1931). Erdtman and Sorsa (1971) described the spores from British West Indies as convex-plane, $22 \times 37 \times 23 \mu$ (perine not included) with the laesura about 21μ , and the perine similar to that in *N. biserrata*. The exine stratification is obscure. Spores from North America (Florida) are subsilate to tuberoso, ellipsoid, monolete, and measure $38\text{--}55 \times 21\text{--}31 \mu$ (Kremp & Kawasaki, 1972).

Harris (1955) described the spores of the New Zealand *Nephrolepis cordifolia* as having verrucate surfaces with elongated projections and of $18\text{--}40 \mu$. Spores of the same species in India (Darjeeling) are reported to be bilateral and possess a very thin perine forming small humps (Sen & Sen, 1973).

Some other species of *Nephrolepis* have also been described by Erdtman and Sorsa (1971). For example, the spores from Java of *N. davallioides* (labelled as *N. acuminata*) are provided with a more or less verrucose, dark brownish, cf. perinous layer $ca 1.0 \mu$ broad. The spores are reported to be concavo-convex and of $17 \times 34 \times 23 \mu$ in size (perine not included). The Ceylonese species of *N. biserrata* has convex-concave spores and measured $23 \times 39 \times 26 \mu$ (perine included). It has a perine $ca 1.5 \mu$ thick, is verrucose; warts are dark brownish $ca 1.3 \times (2.0\text{--}6.0) \mu$ high. The Japanese species of *N. falcata* has a more or less perinous thickening which is columnar, wart-like and about $(3.0\text{--}4.0) \times (4.0\text{--}7.0) \mu$. The spores are $30 \times 45 \times 35 \mu$ (perine not included). The Ceylonese species of *N. hirsutula* has convex-plane or slightly biconvex spores, $21 \times 35 \times 25 \mu$ thick and finely verrucose.

The bilateral and more or less verrucate sculptine patterns of the spores is similar, if not identical, in all species of *Nephrolepis* so far examined, and thus form a rather homogeneous group by themselves. Though a few of the *Nephrolepis* species are remarkably variable, poorly defined or with bizarre features, the uniformity and uniqueness in their vegetative characters, however, has clearly demonstrated the naturalness of the whole group (Pichi-Sermolli, 1965). "It therefore constitutes a clearly natural genus" (Copeland, 1958).

Traditionally *Nephrolepis* has been associated with the Davallioids, Dicksonioids or the Aspidioid ferns. Copeland (1947) commented that this genus has many morphological and anatomical characters in common with the Davalliaceae and affinity seems certain, but many are not close. In chromosome number ($n = 41$), scales (peltate) and indusium (reniform), *Nephrolepis* resembles *Oleandra*; but in many other characters, such as habit, anatomy of the stem and stipe, articulation of the stipe, the feature of the rhizome, venation, position of the sori and structure of the spores, they differ considerably (Pichi-Sermolli, 1965). However, as a group, this genus has spores similar to its closest relative of Davalliaceae ferns, *Davallia*, *Humata*, *Araiostegia*, *Leucosteiga* and *Davallodes*, all of which possess spores with markings of varying degree. Undoubtedly, the phylogenetic position of *Nephrolepis* is thus in the Davalliales.

Since features of some *Nephrolepis* species are similar to some of the fern genera and families, especially members of the Davalliaceae, and have in the meantime shown to be distinctive in other important characters, it might be better to group all the species of *Nephrolepis* in a separate and distinctive group, the family Nephrolepidaceae, as was suggested by Ponce de Leon (1935). The phylogenetic affinity of this family is with the family Davalliaceae.

II. *Oleandra*

The bilateral spores of the genus *Oleandra* are also homogenous in having a distinctive, thick, smooth or wrinkled perine with a few or many protruding folds. The folds may form an irregular network having large meshes (lophate). Spinulose excrescences distributed on the surface may be few or numerous. Usually these

are broader and thicken at the base tapering to sharp apices. Some of these structures have blunt rods.

In the literature, all workers who have done palynological work on *Oleandra* have reported similar findings. For example, Erdtman and Sorsa (1971) described the convex-plane spores of *O. musifolia* of Ceylon as being $28 \times 40 \times 30 \mu$ (perine not included), the perine with folds of $ca\ 5.0\text{--}10.0 \mu$ high, and anastomosing to form irregular polygons with broadly conical and blunt crests. The perine is sparsely spinulose or dentate. It is provided with densely spaced, intra-perinous rods about $(2.0\text{--}5.0) \times (0.5\text{--}1.0) \mu$ and spaced $ca\ 1.0\text{--}2.0 \mu$ apart. As described by Kremp and Kawasaki (1971) the ellipsoid spores of the Javanese *Oleandra neriiformis* measure $43\text{--}63 \times 36\text{--}49 \mu$, and are monolete and perisporate or psilate (in this case, presumably the perine has sloughed off!). Erdtman (1957) also illustrated the spore of this species. Copeland (1947) mentioned that the spores are bilateral or angular by shrinkage of the episporium and are apparently smooth. Sen and Sen (1973) illustrated and described the spores of Indian species of *O. wallichii* as monolete, bilateral plano-convex in lateral view, and oblong in polar view. The perine is said to be folded and spiny.

The habit of growth of *Oleandra* is almost unique and has been described as the only shrubby fern, although all species included in it are not necessarily shrubby (Nayar, Bajpai & Chandra, 1968). The genus also shows homogeneity in many features, such as spore sculpture, etc. It differs from all other ferns in the anatomy of the stem, the position of the sori, the presence of peculiar aerial roots, and also in the structure of the spores (Pichi-Sermolli, 1965; Braggio, 1966). There are thus enough justification to treat *Oleandra* as an isolated genus in the independent family Oleandraceae Ching ex Pic. Ser., as agreed by many pteridologists (J. Smith, 1866; Diels, 1889; Christensen, 1938; Ching, 1940).

The ancestry of *Oleandra* is unknown (Copeland, 1947). Its remarkable resemblance in many features with some species of *Davallia* and *Humata* suggests clearly its close affinity with the Davallioid ferns. Nowadays, most workers place it under the Davalliales.

In ferns, bilateral perinate spores are characteristic of the Aspidioids, Asplenioids, Lomariopsidoids and the Thelypteroid ferns, and the presence of spinulose excrescences over the perine is found especially common among the Aspidioid genera (Nayar & Devi, 1964; Nayar & Kaur, 1965). When the characters of the spores are taken into consideration with anatomical, morphological and cytological features, it is suggested that this unique group of ferns has a closer phylogenetic relationship with the Aspidioid ferns, as has been suggested by many investigators such as Presl (1836), Dickson (1946), Nayar, Bajpai and Chandra (1968), and Pichi-Sermolli (1965). The last author has also emphasized that its affinity in the second place is with the Polypodiales, rather than with the Dicksoniales to which affinity was alluded by most authors in the past.

III. *Arthropteris*

Copeland (1947) referred to the spores of *Arthropteris* as oblong and with episporium. In his study on the genus of *Arthropteris* in Malasia, Holttum (1966) mentioned that the spores of this genus have folded perispores.

However, there are some differences of opinion concerning the sculptine structures even within the same species. For example, Harris (1955) reported the New Zealand species of *A. tenella* as having bilateral, winged spores with cristate perispore separated from the spore wall and both of these structures differ in contour. The surface is striate-scabrate and with a few crests. The crests, when seen in oblique or transverse view, form irregular, almost spinulose projections, $9\text{--}14 \mu$ in height. The contour or outline is deeply resected. However, spores of

the same species from the same country were reported by Sen and Sen (1973) to be monoletе-bilateral and possessing a thin and granulose (in the description) or verrucose (in the diagram) perine. Furthermore, Kremp and Kawasaki (1972) reported this same species to have monoletе ellipsoid spores of $34\text{--}62 \times 27\text{--}43 \mu$, and having a thin perine with psilate surface. Our SEM investigation on *A. tenella*, however, confirmed the correct observation and description of Harris (1955). The verrucose spores of Sen and Sen (1973) were most probably due to contamination or observation on abnormal spores. Those observations by Kremp and Kawasaki (1972) could have been either too immature or mature spores with ablated perine, a phenomenon frequent among many *Arthropteris* species.

Spores of several other species of *Arthropteris* have been studied e.g. *A. altescandens* of Juan Fernandez was reported to have spores with short elliptic to subcircular amb and as having a very thin (*ca* 0.3μ) and folded perine (folds up to 10μ high). Those of *A. obliterata* (labelled as *Nephrolepis ramosa* Moore) of Ceylon was said to have no perine, were biconvex and $39 \times 55 \times 40 \mu$. The psilate spores of *A. monocarpa* of Africa and Madagascar and the spores with a large and folded perine and smooth exine of the African (Congo) *A. orientalis* have also been studied by Braggio (1966).

The affinity of *Arthropteris* is not clear. Copeland (1947) placed it tentatively in the Oleandra-Davallia series. Collective similarities in aspects of frond structure, articulation of pinnae, terminal sori on veins, are evidence of affinity with the *Nephrolepis*. Holttum (1966) does not think that *Nephrolepis* is its nearest relative despite the placement near *Arthropteris*. He, however, agreed with J. Smith in accepting *Arthropteris* as a natural genus, and believed that its peculiar combination of characters may give significant hints as to interrelationships among various groups of ferns. But, he is not yet clear as to how such a relationship may best be formally expressed in a scheme of classification. From studies on the spores of two *Arthropteris* species of Africa and Madagascar, Braggio (1966) emphasized that *Arthropteris* differs from both Oleandraceae and Davalliaceae, and that it ought to be referred to the order of Aspidiales because of its spore characteristics (with psilate exine and a wide and thin perine, with or without ornamentation).

From our observation on spore structure *Arthropteris* species is closer to the Oleandroids rather than to the *Nephrolepis* and Davalliaceae. This is especially evident from the spores of *A. articulata* which are almost indistinguishable from those of some *Oleandra* species (Plate V, figs. 46–49). Spores of other species of *Arthropteris* may not be more distant as they possess a smooth exine and a thick and variously folded perine with different sculptured patterns (Plate VI). However, they still display numerous structural features in common with the *Oleandra* spores. Pichi-Sermolli (1965) also pointed out the similarities of both genera, such as the articulation of the stipe, the shape of the sorus and indusium, the presence of a wide perine, and the chromosome number. When everything is taken into consideration, the disposition of *Arthropteris* in the Davalliales is undoubtedly natural.

The proper systematic position of the peculiar monotypic genus *Psammiosorus* (endemic in Madagascar) is not fully established (Christensen, 1932; Copeland, 1947; Tardieu-Blot, 1964; Pichi-Sermolli, 1965; Braggio, 1966; Holttum 1966).

In conclusion, the family Davalliaceae sensu Copeland (1947) can now be envisaged as the order Davalliales which comprises three natural groups, the family Davalliaceae s.s, containing more strictly Davallioid genera, the family Oleandraceae, with the genera *Oleandra* and *Arthropteris*, and the family Nephrolepidaceae, with the monotypic genus *Nephrolepis*. The proper phylogenetic position of *Psammiosorus* cannot be proposed until further study. At the level of the Order, the affinity of the Davalliales is close to the Aspidiales.

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